

The University of Chicago

SOME EFFECTS OF ETHYLENE
ON PLANTS

A PART OF THE DISSERTATION SUBMITTED
TO THE GRADUATE FACULTY IN CANDIDACY
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

By
HERBERT SNOW WOLFE

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THE BOTANICAL GAZETTE

December 1931

EFFECT OF ETHYLENE ON THE RIPENING OF BANANAS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 424

HERBERT S. WOLFE

(WITH EIGHT FIGURES)

Introduction

The gas ethylene has many effects on animals and plants similar to those produced by ether, but differing also in many respects. It has been known for over a century and its anaesthetic and toxic properties have been understood for fifty years, but only within the last decade has it come into such prominence as ether has enjoyed for much longer. In this period it has found extensive employment commercially for the hastening of fruit ripening, both real and apparent. As is often the case with rapid development of a new aid to industry, however, practical application has outrun cautious investigation, and the literature mostly contains only qualitative experiments on the effects of ethylene on fruit ripening. Nothing is known of the way in which this stimulation of the ripening process is made effective, nor of the range within which it may be attained. Since the ripening of fruit is largely a process of enzymatic transformations, it was thought that an investigation of the effect of ethylene on the activity of the enzymes in the fruit might throw light on the mechanism of the stimulative effect. Earlier work on the ripening of tomatoes with ethylene, reported to the West Virginia Academy of Science in 1928, showed striking relations between enzyme activity and the ethylene treatment.

Since bananas had been widely advertised as showing marked response to ethylene in ripening, an investigation was begun of the effect of this gas on the enzymes in this fruit. To the writer's surprise, preliminary work showed that it was not possible to obtain appreciable differences consistently between treated and untreated lots. This raised the question as to the validity of the widely accepted fact of accelerating the ripening of bananas with ethylene, and accordingly the investigation was changed to a quantitative study of the chemical changes in the banana during ripening with and without ethylene.

The use of ethylene for ripening fruits had its inception in the discovery by DENNY (7) that the effective agent in the coloration of lemons by the fumes from oil stoves was the ethylene content of those fumes. Shortly after this HARVEY (12) announced that celery could be blanched profitably by the use of ethylene, and later in the same year ROSA (29) reported on the acceleration of ripening of tomatoes by ethylene, the first case of its use for fruit ripening. HARVEY (13) also reported that green bananas could be ripened to yellow in not more than 48 hours, by introducing one part of ethylene for every 1000 parts of air in the ripening rooms, and this at 18° C. Besides the advantage of reducing the storage time to half, the new process was said to save loss in weight through the shorter holding time, and loss from decay because of the lower holding temperature. Since the first report, HARVEY (14, 15) has published a number of popular articles on the ripening effect of ethylene on bananas and other fruits which are shipped in the green condition; but no chemical analyses seem to have been made by him in support of the observations on the apparent acceleration of ripening in these fruits.

A few others have tried the effect of ethylene on bananas. CHASE and CHURCH (5) made analyses of fruits ripened with and without ethylene, and reported no effect (except color) for citrus fruits and dates, while persimmons showed definite acceleration of ripening. The two experiments on bananas were so unsatisfactory with regard to the conditions under which they were carried out that no analyses were made of them. HIBBARD (16) has recently reported on a few experiments with bananas, and a single set of analyses is given. The

unsatisfactory nature of these analyses and of the conclusions drawn from them will be pointed out later.

There exists, then, only one published set of analyses of bananas ripened with ethylene, and these are open to question. The normal ripening process, however, has been analyzed repeatedly during the last three-quarters of a century, beginning with the work of *BUIGNET* (4) in 1861. The more important of these references prior to 1914 are listed by *GORE* (10), and will be given here only when they are pertinent. The analyses of *GORE* were by far the most thorough which had been made up to that time, and were made, as he states, "because an accurate account of the chemical changes for use in exact bio-chemical studies was . . . lacking." Unfortunately an error in method invalidates the results of his labors so far as sucrose and reducing sugars are concerned; and, like the majority of his predecessors, he failed to give the variety of banana with which he worked.

The best series of analyses available today is that of *BOURDOUIL* (3) for the Cavendish banana. *THOMPSON* (33) has given a few analyses for this variety also, while *MYERS* and *ROSE* (21) have published a set of analyses for the Gros Michel variety. This last set is open to considerable question, as will be shown later.

Materials and methods

SOURCE OF FRUIT.—In the present investigation only the Gros Michel variety, the ordinary banana of commerce in the eastern United States, was used. Through the kind cooperation of the United Fruit Company, one bunch of green bananas was supplied each week for 8 weeks for this work, and grateful acknowledgment is made to this company, and to Mr. J. H. *LEATHERS*, the manager of the Chicago office of its distributing subsidiary, the Fruit Dispatch, for courtesies extended. Directions were given to the foreman of the banana rooms to select as green a bunch as possible each Monday and send it to the laboratory. Unfortunately it was not learned at first that on Monday there were available only bananas which had been held since Saturday in the cold storage rooms, of which the greenest was delivered weekly for series D to H. Later, series I, K, and L were run on bananas delivered from new shipments as they

were received in Chicago on Tuesday, and were thus somewhat greener than the previous lots. Series M was carried out in the commercial ripening rooms of the Great Atlantic and Pacific Tea Company, and I am indebted to the manager of their warehouses in Chicago, and to the foreman of the banana rooms, for making possible this trial of commercial conditions, as a check on laboratory experiments.

METHOD OF SAMPLING.—In series D to I, hands of bananas were cut from the bunch as soon as it was received, and each hand was divided in halves, one for treatment and one for control. The hands of the bunch were numbered in Roman numerals from the top of the bunch downward, and the fingers of each hand were numbered in

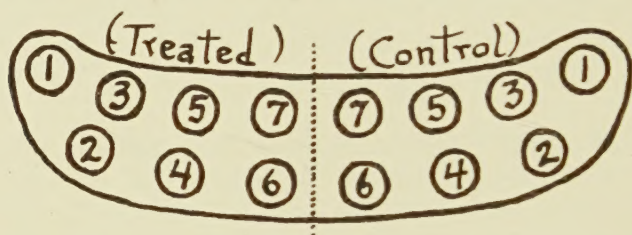


FIG. 1.—Diagram of cross-section through hand of bananas, showing scheme of numbering fingers in half hands.

Arabic numerals from the outside toward the center (fig. 1). A sampling scheme was devised which seemed to eliminate variation due to the position in the hand and of the hand on the bunch in the samples for analysis. The bunches were of seven or eight hands, and hands II to VII were always used for analysis. Thus each sample consisted of six bananas, as nearly comparable as seemed possible to the bananas of the corresponding sample and to the other samples of the series. The method of sampling was to take on the first day bananas II-1, III-2, IV-3, V-4, VI-5, and VII-6, on the second day II-6, III-1, IV-2, V-3, VI-4, and VII-5, etc.

METHOD OF RIPENING.—The two sets of half hands were placed in two large galvanized iron containers of 100-liter capacity, each provided with a water seal around the cover and gas cocks at the top and bottom of opposite sides. The bananas were supported on racks of galvanized wire mesh within the cans, so that they were evenly

distributed through the volume of the containers. To one can was introduced an amount of ethylene sufficient to give the desired concentration within the can, using a mercury gas burette. This amount was 100 ml., giving a 1:1000 concentration, in series D, E, F, G, and I; and 10 ml., or 1:10,000, in series H. The other can served in all cases as a check.

In series K and L it was desired to use higher concentrations of the gas, and for these series cans of 25-liter capacity were used, as well as the larger ones. Since more than two conditions with respect to ethylene concentration were desired simultaneously in these series, it was necessary to vary the method of sampling a little. In these series, therefore, the control can received as before all of one set of half hands. The corresponding treated half hands were paired II-VII, III-VI, and IV-V, so as to neutralize so far as possible the influence of stem position on the rate of ripening (really the influence of the age of the hand); and the same finger was taken from all the half hands for each set of samples. Furthermore, the fingers of the control half hands were analyzed in corresponding pairs, instead of all together. Thus the samples for analysis are more comparable for the treated and control of any treatment on a given date than are the samples from the various treatments; but all samples on a given date are closely comparable.

The samples for series M were taken as for series D to I, but the half hands were hung in different ripening rooms, each of about 500 bunches' capacity and filled with bananas. One of these rooms had ethylene released in it each evening for 3 days, in quantity sufficient to give about 1:1000 concentration. This treatment was carried out by the engineers in charge of the ripening rooms in their regularly accustomed manner.

The temperature in series D-F and H-L was maintained constantly at $22^{\circ}\text{C.} \pm 0.5^{\circ}$, these series being run in a basement room with electric heaters thermostatically controlled. A thermograph checked the temperature regulation. Series G was run at a temperature varying between 17° and 20°C. , and series M at 18° - 19°C.

Aeration of the cans was accomplished every 12 hours during the more active period of ripening, an electric fan assisting the completeness of this operation. Analyses of the air in the cans showed that

the content of CO_2 never reached more than 10 per cent at any time, thus assuring that a plentiful supply of O_2 for normal ripening was always present. In the earlier series of experiments the CO_2 analyses were made only for the purpose of ascertaining whether the O_2 content was sufficient, but in series H to L the bananas were weighed regularly and respiratory activity determined also. Humidity within the ripening cans exceeded 95 per cent R.H., as indicated by numerous hygrograph records. Maximum-minimum thermometers laid among the bananas inside the cans showed that even during the most active period of ripening there was never a rise of temperature within the cans greater than 1°C .

METHOD OF ANALYSIS.—The samples for analysis were weighed, carefully peeled, and the weight of peel and pulp determined separately. The pulp was at once passed through a fine food chopper if it was green, or a vegetable ricer if it was ripe, and then rubbed up quickly in a mortar. Portions of 10–15 gm. were then dished out in duplicate into tared Erlenmeyer flasks of 125 ml. capacity, stoppered with tared corks, and these were at once weighed. Then 0.5 gm. of CaCO_3 was added to each flask and 50 ml. of boiling 95 per cent alcohol was poured in. After rapid mixing of the contents, the flasks were put on a hot plate and the contents boiled for 5 minutes. The whole procedure was so standardized that, except in part of one series, as explained later, the time from peeling the banana to pouring on the boiling alcohol took almost exactly 10 minutes. The flasks were cooled and stoppered, and put away in the dark until ready for the analysis.

The analysis was made for three constituents only: reducing sugars, total sugars (from which sucrose was calculated), and starch. The preserved samples were filtered off with suction, the liquid being carefully decanted from the solid matter in the flask. The residue was then treated with four successive portions of hot 80 per cent alcohol, and after the fourth decantation the solid matter was pressed onto the filter. Qualitative tests showed that the filtrate from this fourth washing was free from sugars. The alcohol on the samples was boiled gently between each two washings, to increase the certainty of the extraction of all sugars. The combined filtrates were freed from alcohol in the usual manner on the steam bath, made up

to volume, and filtered. Aliquots were taken for direct determination of reducing sugars and for acid hydrolysis to determine non-reducing sugars. For this latter operation, 1 ml. of concentrated HCl was added to 10 ml. of the original solution, and the mixture was put at 25°C. for 24–48 hours. It was then almost neutralized to litmus, made up to volume, and aliquots taken for reducing power. Non-reducing sugars were calculated by difference in the usual way and expressed as sucrose. All determinations of reducing power were made by the Bertrand modification of the Munson-Walker method. The residue after extraction of the sugars was dried to remove all alcohol and transferred to a 500 ml. Kjeldahl flask. To this, 200 ml. of water and 12.5 ml. of concentrated HCl were added and the mixture heated on the steam bath under a reflux condenser for 3–5 hours, depending on the ripeness of the sample. It was then cooled, nearly neutralized to litmus, made up to volume, and filtered. Aliquots were taken for reducing power, as glucose, and the results calculated as starch. Preliminary studies, in which the action of saliva, Taka-diastrase, 0.5 per cent and 2.0 per cent HCl were compared, showed that the 2 per cent HCl gave the same yields as the two enzyme procedures, whereas the 0.5 per cent HCl gave lower yields. Since the acid hydrolysis was much the simpler and more uniform method, it was adopted as accurate.

Moisture content was determined at each sampling on a sample taken simultaneously with the samples for carbohydrate analysis. These moisture samples were weighed, put in a drying oven at 105°C. for 30 minutes to stop enzyme action, and finally dried for 20 hours in a vacuum oven at 70°C.

All results have been recalculated to the basis of the original fresh weight of the banana pulp, since that mode of expression has been employed consistently by nearly all previous investigators.

Experimental results

COLOR CHANGES.—The most obvious change during the ripening of bananas is the change in color from green to yellow, and finally to brown in the overripe fruit. Table I gives briefly the salient observations on the rate of color change with and without ethylene. In no case did the control bananas lose a remnant of green persisting at the

distal end of the fruit before the close of the experiment, whereas this had long before disappeared from the treated fruits. Indeed, this persistent green tip in the controls was the most striking feature of the difference in color. The treated fruits attained a true yellow all over the peel some 12-24 hours before traces of green elsewhere than at the tips had ceased to be visible on the controls. But the difference in degree of color was small in all cases except in series L, where the controls were still green all over, and oozing latex when cut, at the end of 72 hours. In all other series it was possible for disinterested observers to distinguish treated from untreated samples at the end of 48 hours, but the difference was never very striking nor

TABLE I
RATE OF COLOR CHANGE IN BANANAS RIPENED WITH AND WITHOUT ETHYLENE

SERIES	COLOR AT START	HOURS UNTIL GREEN IS GONE FROM TIP OF FRUIT		HOURS UNTIL BODY OF FRUIT IS BRIGHT YELLOW	
		Control	Ethylene	Control	Ethylene
E.....	Light green	100	60	84	72
F.....	Light green	120	60	96	72
G.....	Brownish green	120	72	120	96
H.....	Light green	190	60	72	60
I.....	Dark green	168	72	120	120
K.....	Dark green	168	84	120	96
L.....	Dark green	168	84	168	120

of large degree. It was noticed that treated bananas always lost the green and developed the yellow rather uniformly over the whole body of the fruit, whereas the controls yellowed first in the middle and then increased in yellow toward the tips. Series G was run with bananas which were a brownish-green at the start and were only a dirty yellow at ripeness. It seems probable that they had been chilled in shipment, from the symptoms observed.

CARBOHYDRATE CHANGES. The data from analyses divide naturally into three groups, according to the ethylene treatment given and the temperature used: those for 1:1000 ethylene at 22°C., those for the same concentration but at 18°C., and those for various concentrations at 22°C. All analyses were made on duplicate samples, and the average of these two is the value given in all cases. Tables II and IV give the analyses for total sugars and for starch at various

stages of ripeness with air alone and with 1:1000 of ethylene in the air at 22°C. Four separate series of analyses are involved, in three of which the bananas were no longer fully green at the start, whereas in the remaining one they were as green as it is possible to receive them in Chicago. In series D, however, both lots received ethylene

TABLE II

TOTAL SUGARS AS PERCENTAGE FRESH PULP WEIGHT AT 22°C.
WITH 1:1000 CONCENTRATION OF ETHYLENE

SERIES	TREATMENT	HOURS AFTER START OF EXPERIMENT					
		0	24	48	72	96	120
D	{E.....	4.75	11.00	15.80	18.90	20.80	
	{E.....	5.05	10.00	14.40	18.00	20.60	
E	{C.....	4.20	9.62	15.25	18.55		
	{E.....	4.44	10.75	16.55	19.15		
F	{C.....	4.90	11.20	16.40	18.90	20.35	21.05
	{E.....	5.40	12.20	17.30	19.50	21.30	21.80
I	{C.....	0.92	3.72	9.50	16.80	21.75	21.50
	{E.....	0.96	4.15	10.00	16.55	21.15	21.10

TABLE III

TOTAL SUGARS AS PERCENTAGE FRESH PULP WEIGHT AT 18°-20°C.
WITH 1:1000 CONCENTRATION OF ETHYLENE

SERIES	TREATMENT	HOURS AFTER START OF EXPERIMENT					
		0	24	48	72	96	120
G	{C.....	4.08	9.17	14.05	18.40	18.80	20.35
	{E.....	4.38	9.54	14.55	18.85	19.40	20.55
M	{C.....	1.00	3.70	6.90	10.20	14.00	17.40
	{E.....	0.90	4.60	8.40	12.20	16.10	19.40

through the experiment. Figs. 2 and 3 show graphically the analyses for all carbohydrates in both treated and untreated lots of series F and I. It will be observed that the various series, although showing slightly different rates of ripening, are rather uniform in showing the ethylene-treated bananas slightly more advanced in ripening (more sugars and less starch) than the controls. In series I, however, this difference is reversed. It is worthy of mention that, in every other

series than this one, the right half of the hand was always taken for the control, but in this series the left half was made the control. The small differences found consistently between treated and control halves seem, in view of the results in series D and I, to be due to in-

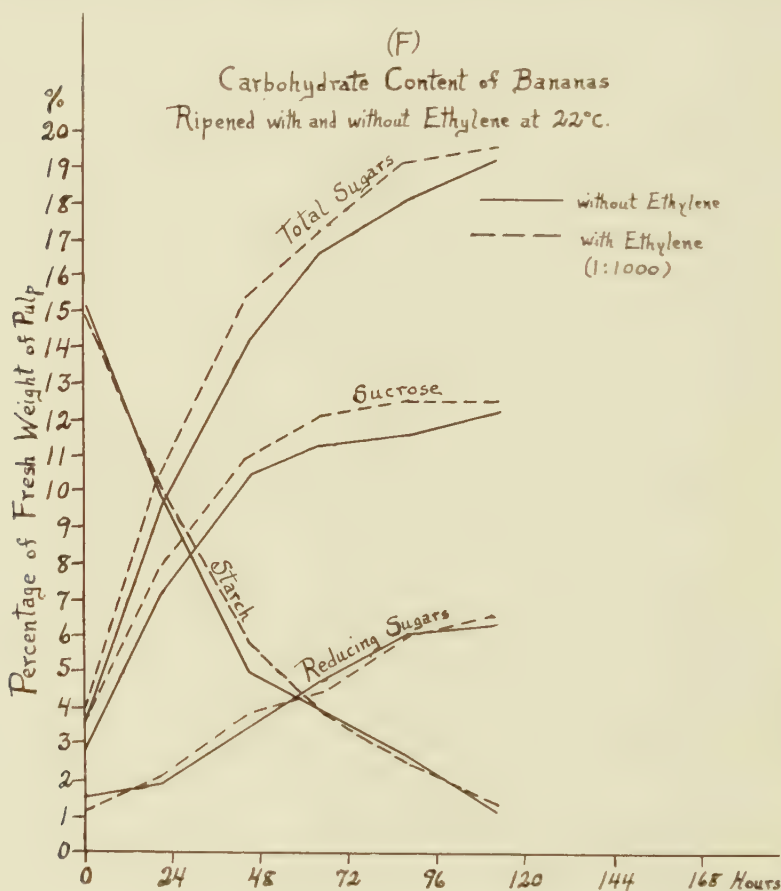


FIG. 2.—Ripening curves for bananas, series F

herent differences rather than to any treatment. In any case, the difference between control and treated fruit never even approximates that between determinations on successive days.

Tables III and V show that at 18°C. the same results are obtained as at 22°C., although the ripening process is somewhat slower at the

lower temperature. The analytical differences, therefore, are even smaller than the color differences observed, with the possibility that they are slightly but consistently in favor of ethylene. There is no difference in the ultimate sugar content of the ripe fruit.

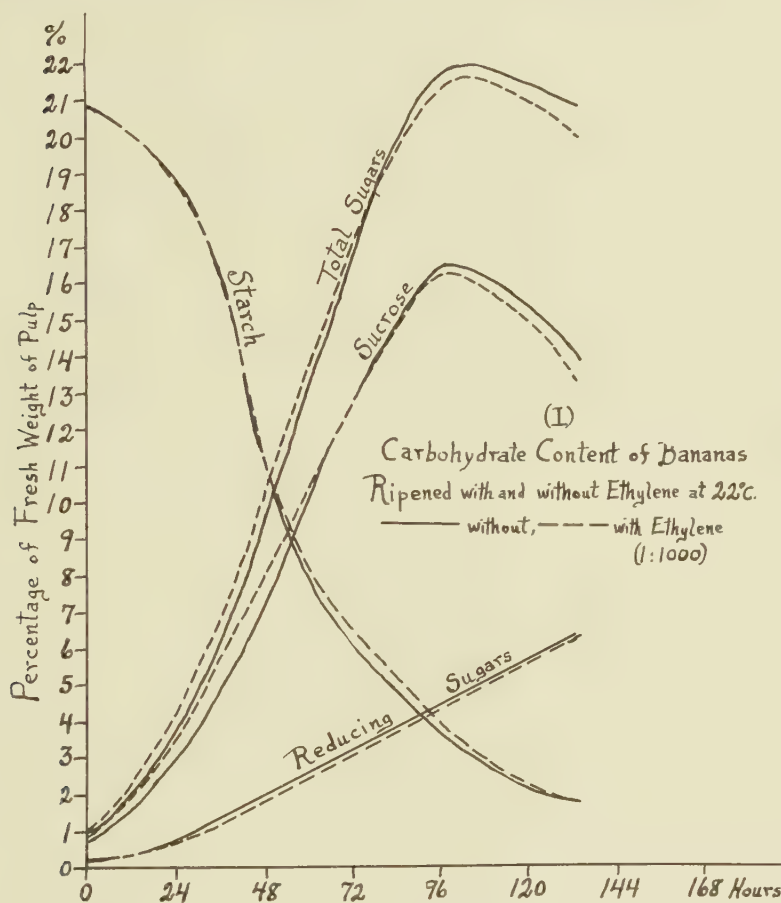


FIG. 3.—Ripening curves for bananas, series I

The results of six rather elaborate series of experiments with different concentrations of ethylene are presented in tables VI and VII. The analyses of series K show no difference between treatment with 1:250 and with 1:500 of ethylene, and the two series seem comparable with series I at 1:1000 and series H at 1:10,000 ethylene. The

difference between control and treated is the same in degree for 1:10,000 and for 1:250 parts of ethylene in the air, and the rate of ripening is the same in each case. Series L analyses show further that even 1:100 of ethylene has no different effect, either in kind or degree, from that of the other concentrations used. The differ-

TABLE IV

TOTAL STARCH AS PERCENTAGE FRESH PULP WEIGHT AT 22°C.
WITH 1:1000 CONCENTRATION OF ETHYLENE

SERIES	TREATMENT	HOURS AFTER START OF EXPERIMENT					
		0	24	48	72	96	120
D	{E.....	17.80	11.00	5.90	3.30	1.40	
	{E.....	16.30	11.00	6.60	3.55	1.40	
E	{C.....	17.87	11.88	6.60	3.36	2.16	
	{E.....	17.05	11.15	6.00	3.00	1.68	
F	{C.....	16.83	10.10	5.30	3.85	2.30	
	{E.....	16.17	10.35	5.95	3.63	2.20	
I	{C.....	20.80	19.00	11.00	6.22	3.55	2.10
	{E.....	20.75	18.60	10.80	6.62	3.95	2.20

TABLE V

TOTAL STARCH AS PERCENTAGE FRESH PULP WEIGHT AT 18°-20°C.
WITH 1:1000 CONCENTRATION OF ETHYLENE

SERIES	TREATMENT	HOURS AFTER START OF EXPERIMENT					
		0	24	48	72	96	120
G	{C.....	18.50	13.60	8.60	4.32	3.12	1.92
	{E.....	18.60	13.75	8.70	4.56	3.12	1.80
M	{C.....	23.05	19.80	16.40	13.00	9.20	5.50
	{E.....	23.10	19.30	15.40	12.60	8.00	4.60

ence between control and treated, however, is very great in all concentrations used in these series (fig. 4). Evidently this difference is due to some peculiar condition within the fruits of this lot, which did not obtain in any other series studied.

Although the controls of series L were greatly retarded, the ethylene-treated bananas ripened at the same rate in these series as in

TABLE VI

TOTAL SUGARS AS PERCENTAGE FRESH PULP WEIGHT AT 22°C.
WITH VARIOUS CONCENTRATIONS OF ETHYLENE

SERIES	TREATMENT	HOURS AFTER START OF EXPERIMENT							
		0	24	48	72	96	120	144	168
H	{Control.	4.10	8.80	14.90	17.60	19.35	19.90	19.45	18.50
	{Ethylene 1:10,000.	4.05	9.25	15.25	18.05	19.90	20.35	18.85	18.90
KY	{Control.	1.73	8.00	14.60	17.25	19.50	20.73	20.50	20.20
	{Ethylene 1:500....	2.40	9.40	16.60	18.70	20.70	21.95	21.00	20.20
KZ	{Control.	1.73	5.00	14.05	17.60	19.60	20.80	20.50	18.70
	{Ethylene 1:250....	2.40	6.80	16.27	18.60	19.90	20.60	20.30	20.00
LX	{Control.	0.85	0.86	0.89	1.20	3.70	12.70	17.00	19.80
	{Ethylene 1:100....	0.95	1.85	7.00	14.50	17.50	19.00	19.90	20.50
LY	{Control.	0.80	0.85	9.90	2.50	6.10	13.35	17.00	19.00
	{Ethylene 1:250....	0.85	2.50	8.20	13.90	18.40	19.50	20.40	21.20
LZ	{Control.	0.85	0.86	1.40	3.20	8.60	13.80	16.50	18.70
	{Ethylene 1:500....	0.90	2.20	6.80	12.10	17.80	18.80	19.45	19.95

TABLE VII

TOTAL STARCH AS PERCENTAGE FRESH PULP WEIGHT AT 22°C.
WITH VARIOUS CONCENTRATIONS OF ETHYLENE

SERIES	TREATMENT	HOURS AFTER START OF EXPERIMENT							
		0	24	48	72	96	120	144	168
H	{Control.	17.40	12.55	8.05	4.20	3.15	2.15	1.55	0.90
	{Ethylene 1:10,000.	17.95	12.30	7.50	3.75	2.75	1.80	1.32	0.90
KY	{Control.	19.65	13.80	7.22	4.40	2.50	1.55	1.20	1.05
	{Ethylene 1:500....	19.30	13.20	6.80	4.10	2.30	1.35	0.85	0.60
KZ	{Control.	19.65	14.60	8.13	4.65	2.55	1.70	1.45	1.40
	{Ethylene 1:250....	19.30	13.60	6.75	4.30	2.10	1.30	1.10	1.05
LX	{Control.	24.00	23.70	23.00	21.60	17.70	10.70	6.50	3.30
	{Ethylene 1:100....	24.00	21.90	16.50	7.70	3.90	2.50	1.70	1.20
LY	{Control.	24.00	23.60	23.10	20.60	15.50	9.00	4.70	2.60
	{Ethylene 1:250....	24.00	21.00	14.00	8.40	4.20	2.65	1.90	1.15
LZ	{Control.	24.00	23.40	22.50	19.50	13.45	8.65	5.20	2.90
	{Ethylene 1:500....	24.00	22.00	15.00	8.60	5.05	3.50	2.40	1.70

all other lots with or without ethylene. Figs. 5 and 6 show that all the curves for sugars and starch can be superimposed rather well, although the point of ripening at which analyses were begun varies

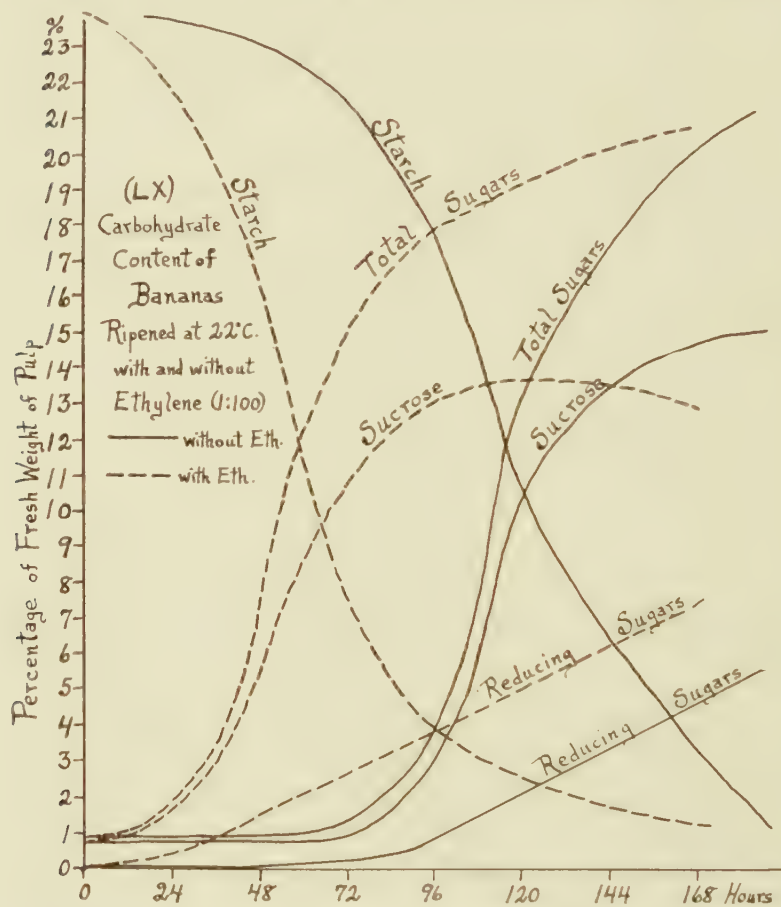


FIG. 4.—Ripening curves for bananas showing dormant stage, series LX

considerably. Indeed, this superposition makes it possible to assign a rather definite point in the ripening process as the stage of ripeness at which fruit was received, the curves for starch, reducing sugars, and total sugars being all in agreement as to the location of this point. These results emphasize the fact that in no case has ethylene

caused fruit to ripen faster than the normal, but has only caused abnormal fruit to ripen normally.

Table VIII gives the results of determinations of respiratory activity of bananas ripening in various concentrations of ethylene,

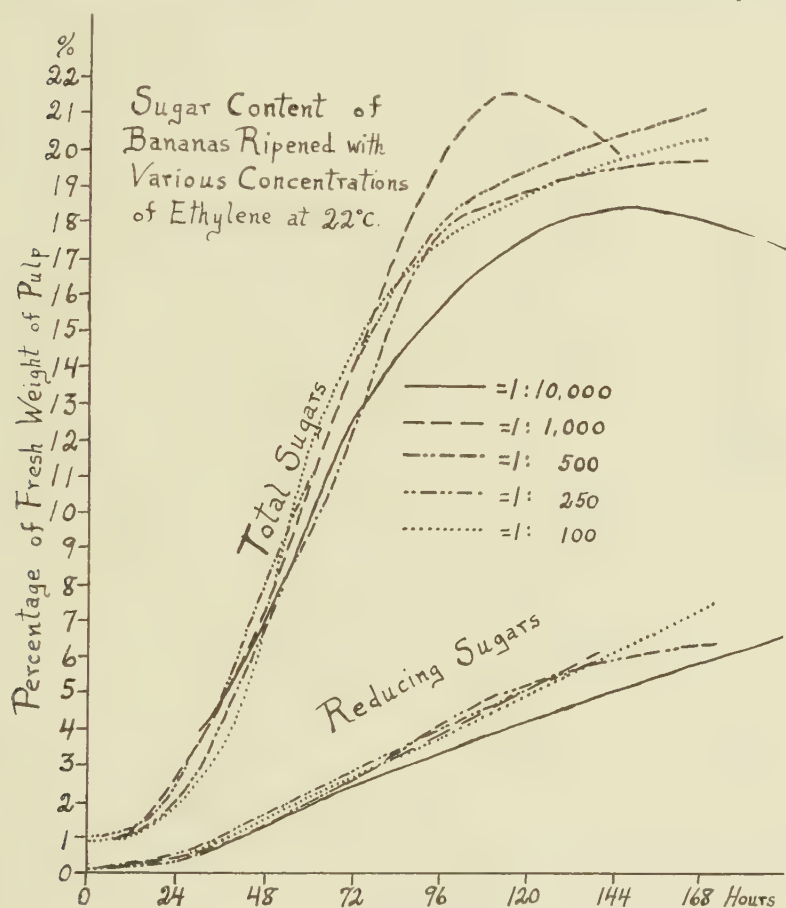


FIG. 5.—Sugars in ripening bananas of several series, curves superimposed

from 1:100 to 1:10,000. The differences between rates of respiration with and without ethylene are too small in degree to be significant, except in the abnormal series L, where the same difference is found as in the ripening rate. There appears to be some suggestion that the respiratory rate increases slightly with increase in the ethylene

concentration; but fig. 7 indicates that the apparent correlation may more probably be made with the difference in rate of starch hydrolysis in the three lots of this series. It should be emphasized that in these graphs the points on the curves for starch and sugar do not

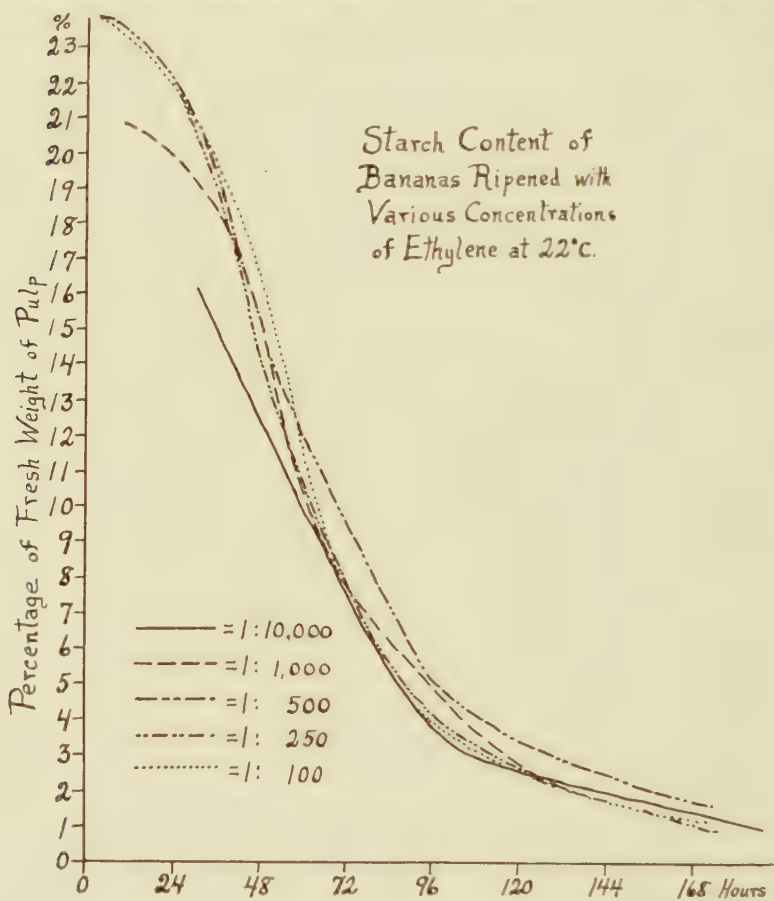


FIG. 6.—Starch in ripening bananas of several series, curves superimposed

represent the content of these substances, but the amount of change in their content during the time interval since the last previous point plotted.

Table IX contains the data on the coefficient of ripeness of the bananas at the time of analysis. The zero points of ripening have

been adjusted in this table in accordance with figs. 5 and 6, so that coefficients shown in different series are for the same stage of ripeness at the same time. The ripe bananas in series L have hardly any

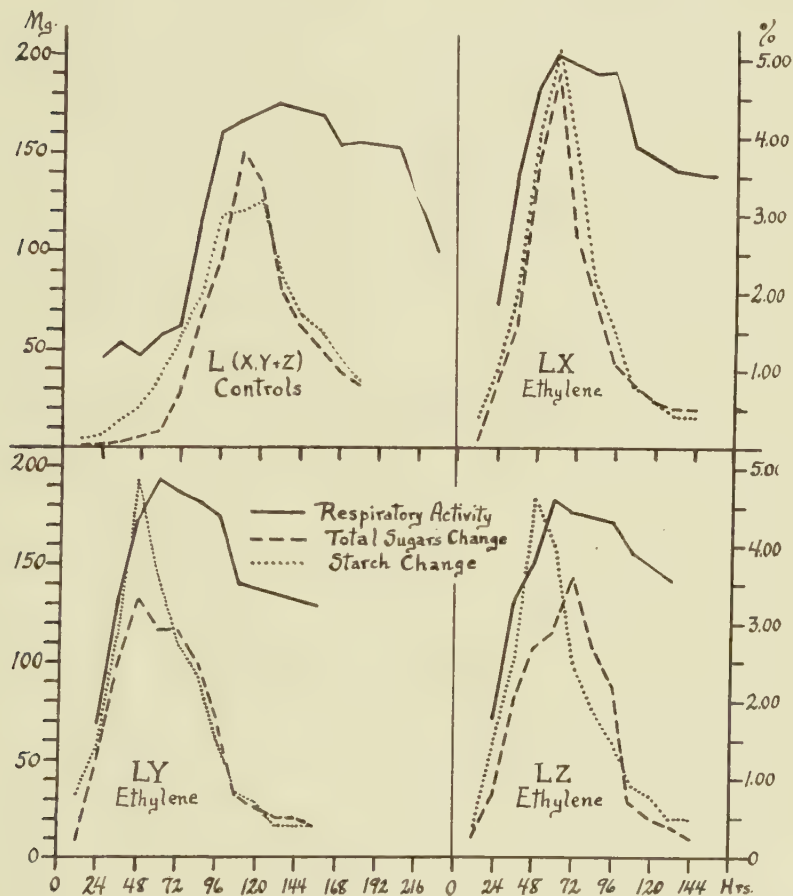


FIG. 7.—Respiratory activity versus starch and total sugar changes in ripening bananas; ordinates for respiratory activity = mg. CO₂ per kg. hr.; for carbohydrates = percentage fresh weight of pulp.

higher coefficient of ripeness than the green fruit of series K. It is evident from this table that only a negative correlation can be drawn between the value of the coefficient and the degree of ripeness of the banana. Within any given series the coefficient increases steadily in

value as ripening progresses, but the rate of increase is hardly the same in any two of the series.

TABLE VIII

RATE OF RESPIRATION AT 22°C. WITH VARIOUS CONCENTRATIONS OF ETHYLENE

SERIES	TREATMENT	MILLIGRAMS CO ₂ PER KG.-HR. DURING INTERVAL IN HOURS AFTER STARTING							
		0-24	24-48	48-72	72-96	96-120	120-144	144-168	168-192
H	{ Control.....	95	132	168	120	136			
	{ Ethylene 1:10,000.	91	130	170	130	132			
I	{ Control.....	75	191	187	180	127	127		
	{ Ethylene 1:1000....	77	195	188	179	132	128		
K	{ Control.....			180	163	112	176	98	
	{ Ethylene 1:500....			188	140	101	126	122	
	{ Ethylene 1:250....			173	138	102	126	126	
L	{ Control.....	45	50	60	138	176	171	155	153
	{ Ethylene 1:100....	74	162	200	192	142	139		
	{ Ethylene 1:250....	68	151	190	178	135	128		
	{ Ethylene 1:500....	71	141	180	172	142			

TABLE IX

COEFFICIENT OF RIPENESS AT 22°C. WITH VARIOUS CONCENTRATIONS OF ETHYLENE

SERIES	TREATMENT	HOURS AFTER START OF RIPENING							
		0	24	48	72	96	120	144	168
F	{ Control.....			1.29	1.44	1.55	1.62	1.67	
	{ Ethylene 1:1000....			1.34	1.50	1.62	1.67	1.72	
H	{ Control.....		1.25	1.34	1.41	1.47	1.52	1.59	1.65
	{ Ethylene 1:10,000.		1.30	1.38	1.44	1.50	1.56	1.62	1.67
I	{ Control.....		1.37	1.48	1.57	1.65	1.72	1.77	
	{ Ethylene 1:1000....		1.36	1.44	1.53	1.62	1.69	1.77	
KZ	{ Control.....		1.50	1.58	1.65	1.73	1.82	1.91	1.98
	{ Ethylene 1:250....		1.50	1.59	1.67	1.77	1.87	1.97	2.04
LZ	{ Control.....	1.23	1.30	1.35	1.37	1.38	1.43	1.50	1.56
	{ Ethylene 1:500....	1.23	1.32	1.38	1.45	1.47	1.49	1.50	1.56
M	{ Control.....	1.30	1.33	1.36	1.39	1.43	1.46		
	{ Ethylene 1:1000....	1.30	1.34	1.38	1.41	1.44	1.46		

Discussion

COLOR CHANGES.—HARVEY (14) has asserted that with 1:1000 ethylene the greenest bananas can be ripened to yellow in 42–48 hours at 18°C., and has published a color plate showing the control still nearly green, with only a trace of yellow, while the treated banana is so yellow-ripe that the peel is breaking. For fruits which are not fully green when treatment starts, a still shorter time is stated to be required for the same result. Even allowing for the fact that “ripe” to the jobber means only “yellow enough to sell,” it has been impossible to confirm these statements in the repeated experiments here reported. Table I shows that even with bananas no longer fully green, at least 60 hours were required; and in all other cases 72 hours was the minimum time for the development of a full yellow color with ethylene, regardless of concentration, and at 22°C. Still longer was needed at 18°C. For really green bananas, 100 hours in ethylene was needed for full yellowing.

These observations were made under laboratory conditions, but they were confirmed and enlarged in the experiment conducted at the Atlantic and Pacific warehouse, series M. At the end of 24 hours the treated and control lots both appeared to be still as green as at the start. After 60 hours the treated lot was slightly more yellow than the controls, but both still showed considerable green in the peel. Examination of the hundreds of bunches which had been ripening simultaneously in the two rooms, with and without ethylene, showed that this slight difference was true in general for the whole contents of the two rooms. Some bunches in each room were still quite green, and some were rather well yellowed, but the average of the two rooms was just about represented by the two experimental lots. So small was the degree of difference that the writer asked the experienced foreman of the banana department to express an opinion, and he agreed that the difference was of very small degree but that it was slightly apparent. There was no question at all, however, that after 60 hours of 1:1000 ethylene treatment at 18°C. (and the engineer in charge gave assurance that the ethylene had been duly administered), many bunches of bananas hardly showed any definite yellowing at all.

CARBOHYDRATE CHANGES. — With regard to the changes wrought within the banana by the treatment with ethylene, it has been stated (14) that a number of fruits, including bananas, are increased in sugar content by 20–30 per cent, and (15) that “fruits ripened with ethylene taste sweeter than those ripened with heat alone.” The present analyses would indicate that color differences of the degree found by HARVEY should correspond, not to 20–30 per cent, but to 100–200 per cent of difference in sugar content. In the analyses of many series of experiments, with various concentrations of ethylene, no difference greater than 10 per cent has been found between treated and control, except in the abnormal series L; and there it was still 300–400 per cent after 100 hours, a phenomenon apparently distinct from any that HARVEY had in mind. Untreated fruits always reached the same ultimate content of sugars as the treated ones, even when doing so more slowly. As to greater sweetness of fruits ripened with ethylene, as opposed to those equally ripe but untreated, the data for the sugars lend little support to the theory. Differences in the quality of treated and untreated fruits are not subject to exact measurement, and the writer can only say that although he sampled the ripe fruits of treated and untreated lots of every series, he could never detect any difference in flavor or quality.

The data which HIBBARD (16) has published are unfortunately those for a single experiment only, which he admits to have been the most striking of all those he performed. In this case two bunches of bananas of the same apparent greenness were compared, one in ethylene and the other in air, at 18°–20°C. As will be seen from fig. 8, both bunches were entirely green at the start, with only about 0.5 per cent of total sugars. The bunch treated with ethylene ripened at a rather normal rate, although more slowly than any in the series here reported. Even series M, at the same temperature, had reached 8 per cent of total sugars in 48 hours, while HIBBARD found only 6 per cent in his treated bunch after 64 hours. But the control bunch had made no more progress toward ripening in 10 days than was made normally in the present series in the first 24 hours. Even the controls of the series L were riper after 4 days than those of HIBBARD after 10 days. Furthermore the total sugars in his analyses never reached more than about half of the maximum value attained con-

sistently in the present investigations. The data given by GORE and by BOURDOUIL are contained in fig. 8 also, and confirm the normality of the present data. Evidently the bananas used by HIBBARD were far from normal, but it would not be safe to assert that the differ-

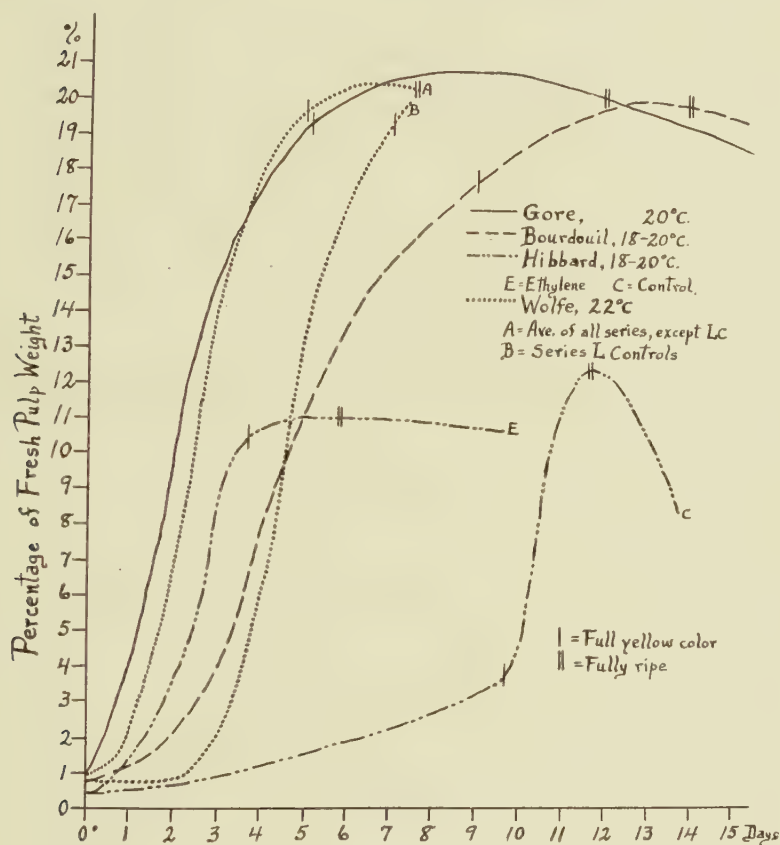


FIG. 8.—Curves of total sugars in ripening bananas as given by various investigators.

ences observed were due to the ethylene treatment. The present analyses prove conclusively that bananas from one bunch, no matter how closely similar in aspect or even in actual chemical analysis, can never accurately be compared with those of another bunch; whereas bananas from the same bunch, if properly selected, will give com-

parable results in differential treatment. Only with such comparable material can trustworthy data be obtained in studies of the effect of different treatments.

There is, however, one undoubted case of acceleration of ripening by ethylene, and that is series L of these experiments. The lots which received ethylene differed no whit in their rate of ripening from those of other series whether treated or not; but the controls showed that ethylene accelerated the ripening process greatly over what it would have been without the gas. Since the controls showed a normal ripening curve once the process had begun, it is evident that the only effect of the ethylene was to cause this process to commence at once instead of delaying several days. If it only initiates the ripening process, it is not unreasonable that bananas already started to ripen should show no acceleration of ripening due to the ethylene treatment. HARTSHORN (11) has suggested that the failure to obtain ethylene stimulation in any other series than L was owing to the ripening process having already begun in all the others. In series I and M, however, the initial stage was apparently the same in degree of ripeness as in series L, as indicated by total sugar content, and these proceeded normally with ripening. A more accurate way of stating the situation would seem to be that only series L had the fruit in a state of quasi-dormancy, from which it is possible for the ethylene to stimulate it.

The question is still moot, therefore, as to whether there is normally any stimulation of the ripening process of bananas by ethylene. Certainly there is none in the case of bananas which have already started to ripen at the time treatment is begun, even though the start has barely been made; although there is a more rapid and uniform development of yellow color. In one out of three bunches of very green bananas, as green as they can be procured in the Chicago terminal, there was found a "dormant" condition from which the ethylene effected a stimulation to ripening at once. But in only this one out of ten bunches, none of which had been held in storage more than two days and each of which was selected as the greenest of several hundred bunches in cold storage, was there any accelerating effect due to use of ethylene. What may be the nature of this "dormant" condition cannot be said, nor how the ethylene operated to

break the "dormancy." It is of interest to note that neither PRINSEN-GEERLIGS (24), working with fruit taken directly from the plant, nor BOURDOUIL, using fruit from the nearby Canary Islands, found any such delay in the start of ripening; and both show by their analyses that ripening had not yet begun in the fruit they used. Since no other sequence of analyses, using green fruit, has been published, it cannot be estimated how rarely this "dormant" condition is found. It might have been possible for the writer to have tested a hundred bunches before another such case of retarded ripening was found; and it would seem that, at least so far as the great inland distributing centers are concerned, there is very rarely received a bunch of bananas which requires ethylene in order to ripen promptly and rapidly. Once ripening has begun, its pace is not affected by ethylene. Whether or not the greater uniformity of yellow color resulting from the use of ethylene is sufficient to warrant its use commercially, is another question entirely; but it should be understood that such uniform yellow color is deceptive as a criterion of the stage of ripeness which has been attained.

SUCROSE AND STARCH IN RIPE BANANAS.—Special interest attaches to these carbohydrates, apart from the question of ethylene effect, because of the varying statements concerning them in the literature. REYNOLDS (27) recently summarized our knowledge on this subject by stating "the ripe pulp contains . . . sucrose . . . as little as 2 per cent or as much as 14 per cent." BAILEY (1) also cited the numerous earlier analyses made by workers of the United States Department of Agriculture as showing a range of 0.2–18 per cent sucrose. Such statements are misleading because they take no account of the methods used for analysis. MIERAN (20) showed by apparently conclusive experiments that the sucrase present in ripe bananas would quickly hydrolyze the sucrose present when the pulp was mashed, unless the enzyme were inactivated at once by heat. In spite of this information, however, many analyses since that time have been made without this precaution, as of course were also many of the earlier ones. The otherwise admirable analyses of GORE are useless, so far as sucrose and reducing sugar values are concerned, because he took no account of the very rapid inversion which takes place in mashed pulp. He was aware that some error existed in his method,

and states that "the values for sucrose are probably slightly high, and those for reducing sugars correspondingly low." Even allowing for the obvious inversion of intended meaning, the "slightly" is a matter of several hundred per cent. The same source of error invalidates the findings of THOMPSON and WHITTIER (33).

In table X are given the sucrose contents of ripe bananas as reported by a number of workers. It will be seen that rarely is the variety specified, and all too seldom is the method of analysis given. In all cases where satisfactory analytical procedure was followed,

TABLE X
SUCROSE AND STARCH CONTENT OF RIPE BANANAS AS
PERCENTAGE FRESH PULP WEIGHT

YEAR	INVESTIGATOR	METHOD	VARIETY	SU- CROSE	TOTAL SUGARS	SU- CROSE AS % OF TOTAL SUGAR	STARCH
1861	Buignet (4)	?	?	10	15	66	?
1876	Corenwinder (6)	?	?	15.10	21.80	70	?
1879	Marcano & Muntz (19)	?	M. paradisiaca	8.50	15.30	56	3.3
1882	Ricciardi (28)	?	?	4.50	24.80	18	0
1893	Mieran (20)	Boiling water	?	12.85	10.05	67	?
1896	Gerber (9)	Boiling water	?	10.45	10.00	55	0.00
1902	Leuscher (17)	?	Gros Michel	15.80	20.30	60	0.95
1908	Prinsen-Geerligs (24)	Boiling alcohol	?	13.70	22.75	60	0.60
1911	Yoshimura (34)	Boiling water	?	8.40	14.05	57	4.25
1911	Reich (26)	Cold water	Gros Michel	5.40	10.35	28	0.75
1912	Bailey (2)	Boiling alcohol	?	5.50	10.00	55	0.71
1912	Thompson & Whittier (33)	Cold water	?	3.50	21.00	16	?
1914	Gore (10)	Warm alcohol	?	5.98	19.15	32	0.82
1914	Thompson (32)	Boiling alcohol	Cavendish	10.70	18.70	57	0.45
1917	Myers & Rose (21)	Boiling water	?	11.12	18.60	60	3.02
1922	Steel (30)	?	Fiji	5.65	24.60	23	trace
1929	Bourdouil (3)	Boiling alcohol	Cavendish	13.11	19.10	67	0.94
1930	Wolfe	Boiling alcohol	Gros Michel	11-13	17-20	64-66	0.8-1.2

however, the sucrose content was found to be over 5.5 per cent. Expressing the sucrose more significantly as percentage of the total sugars found, to take care of the few cases in which very low total sugar values give a deceptive idea as to sucrose content, it is found that sucrose constitutes 55-70 per cent of the total sugars. The bulk of the analyses give about 20 per cent of total sugars, with 11-14 per cent of sucrose.

In the present studies, eight of the ten series of analyses showed a sucrose content of 11-13 per cent at "eating ripe," with a range of 64-66 per cent of the total sugar content. The other two analyses

showed 11–12 per cent of sucrose, but this was only about 56 per cent of the total sugars. In these two series of analyses, series K, an attempt was made to prepare samples for both series simultaneously, instead of sequentially, and so the samples stood for 20–30 minutes before inactivation, instead of for only 10 minutes as in all other series. Because the sucrose values were slightly lower by this method, a return was made in the three series of L to the original method. It can safely be stated, however, that the banana contains between 10 and 14 per cent of sucrose at good eating ripeness, which condition can be described either as when the skin is golden-yellow with tiny brown flecks, or when the total sugars have just passed their maximum. No explanation can be offered for the unusually low values for total sugars reported by a few workers, notably the 10 per cent found by BAILEY and the 11 per cent given by HIBBARD.

The starch content is also given for fully ripe bananas in table X. It will be seen that in the majority of the analyses the starch content is below 1 per cent. MYERS and ROSE (21) reported 3 per cent, but their analysis for the next day gave only 0.7 per cent, a change in rate of starch hydrolysis for this stage of ripeness not found by any other workers. Indeed, the curves for all carbohydrates in their series of analyses agree with those of other workers only up to the sixth day of ripening; thereafter they are so erratic that it is difficult to have confidence in them. The temperature used must have been very low, from the slow rate of ripening, and does not seem to have been controlled at all. The abnormally high starch content for ripe bananas reported by PRINSEN-GEERLIGS (24) must be attributed to his probably having used some small variety of plantain, which does not convert all of its starch. He found a 10 per cent lower water content and a correspondingly higher carbohydrate content than anyone else has reported for bananas. MARCANO and MUNTZ (19) also analyzed a plantain, as they state; and although YOSHIMURA (34) does not state the variety used, his anomalous result may perhaps be thus explained. In his experiment, however, the fruit had not become fully ripe after 21 days “in a warm place.” Thus the starch content of ripe bananas, with the skins beginning to be brown flecked, has repeatedly been shown (in at least 15 analyses) to be less than 1 per cent. The only analyses showing a higher content are

subject to serious question, either as to their having been made on bananas or as to the accuracy of the determination.

In passing, it may be noted that the polarimetric studies of PRINSEN-GEERLIGS, THOMPSON and WHITTIER, and YOSHIMURA are all agreed that there are no sugars found in ripe bananas except sucrose, fructose, and glucose. One of the most tantalizing biochemical problems is how the starch of the banana is converted into sucrose in a few days, in the absence of any demonstrable amylase.

RESPIRATORY RATIOS.—The respiration data are in general agreement with those given by GORE (10), OLNEY (23), and PRINSEN-GEERLIGS (24). The rate is maximum when starch is being most rapidly transformed into sugars, and falls again more slowly as ripening progresses. GERBER (9) gave two sets of analyses, one of which makes a normal curve, while the other hardly rises and falls. The only previous work on the effect of ethylene on the respiration of bananas was done for very short time intervals only, and not through the whole course of ripening. REGEIMBAL, VACHA, and HARVEY (25) showed that when ethylene is added to the air in which a ripening banana is contained, there is quickly a great increase in respiratory activity, followed in a few minutes by a decrease below normal, and then eventually the normal rate is regained. The uniformity with which the data for the respiratory activity of bananas treated with ethylene parallel those for the controls in the present investigations indicates that after the response of the first hour was past, there was no further effect of the ethylene on the rate of respiration. And the effect during the brief stimulatory period is too small to be detected in the output of CO_2 for 12 hours. These observations seem to lend support to the theory of NORD AND FRANCKE (22), that the effect of ethylene on ripening is due in part at least to the increase in permeability of the cells, but the change is only temporary.

These observations, previous and present, are all in considerable agreement for the banana, and are all different from those for citrus fruits. DENNY (8) studied the effect of ethylene on the respiration of lemons, and found that, on the day after the addition of ethylene to the air of the ripening chamber, there was a greatly increased respiratory activity. There was not, however, any effect observable during the 3-5 hours immediately following the introduction of ethyl-

ene, and there was a persistent effect for several days after discontinuing the treatment. This is in contrast with the immediate but brief response given by bananas. MACK (18) has reported finding that ethylene doubled the rate of respiration in celery, but he does not say whether this is an immediate and brief response, such as the Minnesota workers found for bananas, or a retarded but long continued response, such as DENNY found for lemons.

COEFFICIENT OF RIPENESS.—The "coefficient of ripeness" was introduced by TALLARICO (31) some years ago, as an expression of the quotient of pulp weight divided by peel weight. He noted that this quotient steadily increased during ripening, and believed that it afforded a reliable index of the degree of ripeness of the fruit. In the case of the (unnamed) variety with which he worked, small bananas with thin skins, this value ranged from 0.85 to 2.80 during ripening, a range permitting a moderate degree of sensitivity for indicating degrees of ripeness. TALLARICO made no chemical studies in support of his assumption, however, but merely employed the coefficient values to indicate the stage of ripeness of bananas whose enzyme activity he was endeavoring to determine. The term has remained in the literature, and has been employed occasionally, as by BAILEY (2) and BOURDOUIL (3), without any critical examination of the validity of the concept having been made. MYERS and ROSE (21) have recommended a related concept, the peel weight as percentage of the whole fruit, and PRINSEN-GEERLIGS (24) used the complementary concept, the pulp weight as percentage of the whole fruit, from either of which the coefficient of ripeness is immediately derived and both of which are subject to the same errors as is the first term. BOURDOUIL has pointed out that, with fruits of larger size and thicker peel than those used by TALLARICO, the small range of values for the coefficient makes it a not very accurate nor sensitive criterion of the stage of ripeness; but the present investigation seems to be the first to demonstrate the fallacy of the concept. Probably this is owing largely to the fact that almost all of the previous series of analyses have been single and unrepeatable, whereas the ten series in duplicate carried through from green to ripe in the present studies have afforded an opportunity for critical comparison. Besides the data in table IX, the writer has hundreds of determinations of the coefficient for

individual fruits, and these all demonstrate that, even for the fruits of the same hand, the value of the coefficient is not an absolute indication of the stage of ripeness; while for different bunches it possesses no absolute meaning at all. The value is so easily and quickly determined that it would be a most convenient reference point in analytical work if it were trustworthy, but it is not. Only chemical analyses can give any reliable measure of the degree of ripeness of bananas, and it is immaterial whether total sugars or starch content be determined for this purpose.

It is to be regretted that there is no such complete analysis for the Gros Michel variety as BOURDOUIL has given for the Cavendish. The present studies are believed to be reliable, and have been repeated so often as to leave little doubt of their accuracy, but they cover only the period up to full ripeness. The necessity of starting a new series of analyses each week precluded the possibility of carrying any of the series through to the last stages of ripeness.

Summary

1. Bananas ripening in an atmosphere containing 1:1000 parts of ethylene turn yellow at a somewhat more rapid rate than do controls, but the difference is only slight.
2. Such bananas show also a slightly greater increase in sugars and decrease in starch from day to day than do the controls, but the difference is even slighter.
3. Concentrations of ethylene ranging from 1:100 to 1:10,000 all seem equally effective in bringing about the small differences observed.
4. Ripe bananas have 17-20 per cent of total sugars, 10-14 per cent of sucrose, and less than 1 per cent of starch, in both the Gros Michel and the Cavendish varieties.
5. Respiratory activity of bananas treated with ethylene differs little or not at all from that of untreated ones, when 12-hour periods are considered, regardless of the concentration of ethylene used.
6. Rarely there is found a bunch of bananas which is in a quasi-dormant condition, and in this case ethylene stimulates an immediate commencement of ripening, while the controls are delayed several days in starting.
7. The "coefficient of ripeness" is unreliable, as well as insensitive.

8. Comparable results in investigations of the effect of various factors on the ripening of bananas cannot be obtained with bananas from different bunches, no matter how closely similar in aspect, but can be obtained only with bananas properly selected from the same bunch.

These investigations were begun at the suggestion of Professor CHARLES A. SHULL, who has been a constant source of encouragement during their progress; sincere appreciation of this support is expressed. A large part of the work was made possible by the award of the John Merle Coulter Research Fellowship in Botany, and the writer wishes to express his gratitude for this aid.

SUBTROPICAL EXPERIMENT STATION
HOMESTEAD, FLA.

[Accepted for publication August 18, 1931]

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